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Contents

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THE POLYGONAL GRAPH FOR SIMULTANEOUS PORTRAYAL OF SEVERAL VARIABLES IN POPULATION ANALYSIS

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Hutchinson (1936) described the polygonal graph as a means of portraying various related data. While he used this method to depict relationships in a few angiospermous families, no analytical use was made of the method. A later paper (1940) was restricted to the ecological applications of the technique, and the method of comparing climatic zones could well be adapted to the comparison of plant populations (figs. 4, 5, 6). The polygonal graph may serve also as a convenient and useful taxonomic technique in population analysis.

CALYX LENGTH
STYLE LENGTH
COROLLA LOBE
COROLLA TUBE
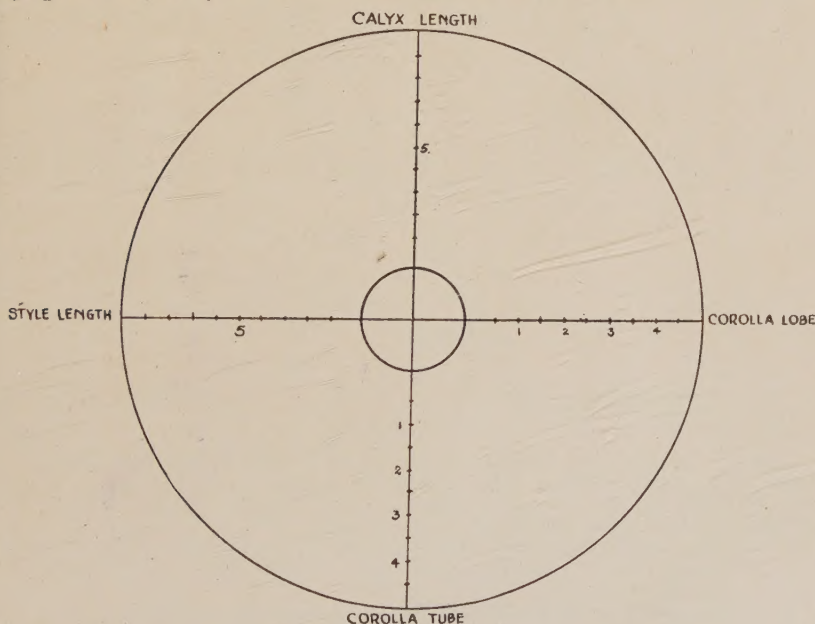
Fig. 1. A base for the polygonal graphing of four characters, using absolute measurements. The radii have been calibrated so that the expected range of variation covers most of each radius.

In population analysis, a taxonomist is generally concerned with determining whether a population contains two or more segregates or merely one variable entity. This may be determined by a fairly large series of two-dimensional graphs, such as curves, bar graphs, or scatter graphs, or by a single polygonal analysis.

The advantage of polygonal graphing is that members of an entire population may be compared in a number of varying characters at a glance. The completed figure in a polygonal graph readily supplies the following data:

(a) the range of variation in any one of three to ten characters.
(b) the mean of any character.
(c) the occurrence of a bimodal distribution in any character.
(d) the correlation between any two of the characters plotted.
(e) the validity of a character in delimiting proposed segregates.
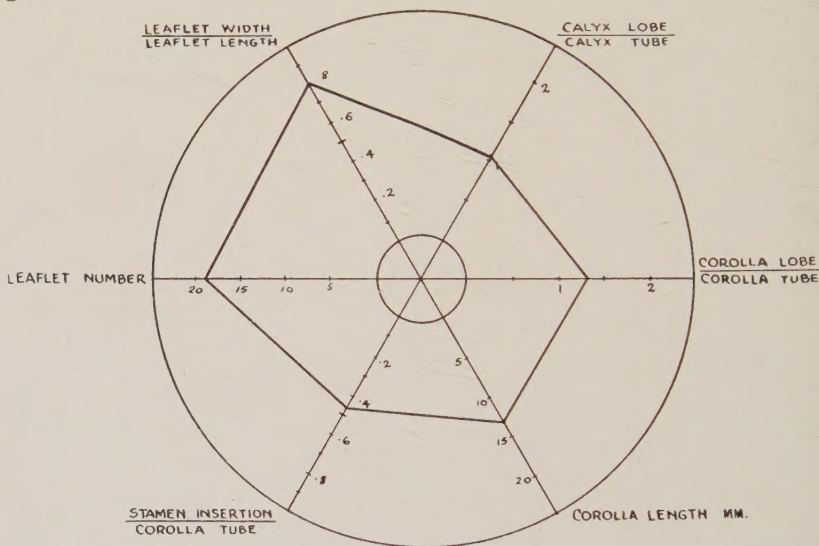
Fig. 2. A base for graphing six characters, some being absolute measurements, some being relative. The ratio leaflet width over leaflet length is an approximation of the more qualitative concept of leaflet shape. The single specimen plotted shows the following characters:

Calyx lobe subequalling the calyx tube.
Corolla lobe 1.3 times the corolla tube.
Corolla 13 mm. long.
Stamens inserted slightly below the middle of the corolla tube.
Leaflets 19.
Leaflets 0.8 as broad as long.

Basically the graph consists of a circle, with as many radii as there are characters to be compared (fig. 1). The characters, measured along each radius, are assigned absolute, relative, or arbitrary values. The characters possessed by each specimen are plotted along each radius, and the points so plotted are joined. Thus each specimen is represented by a polygon (fig. 2), and the entire population is represented by the polygons plotted on the same or similar bases.

The choice of characters is important, and normally those which are thought to possess "keying possibilities" are chosen. However, if many characters are used, separation of entities may be accomplished on one or more of the criteria utilized. In practise, using a circle 10 cm. or more in radius, fifty or more speci-
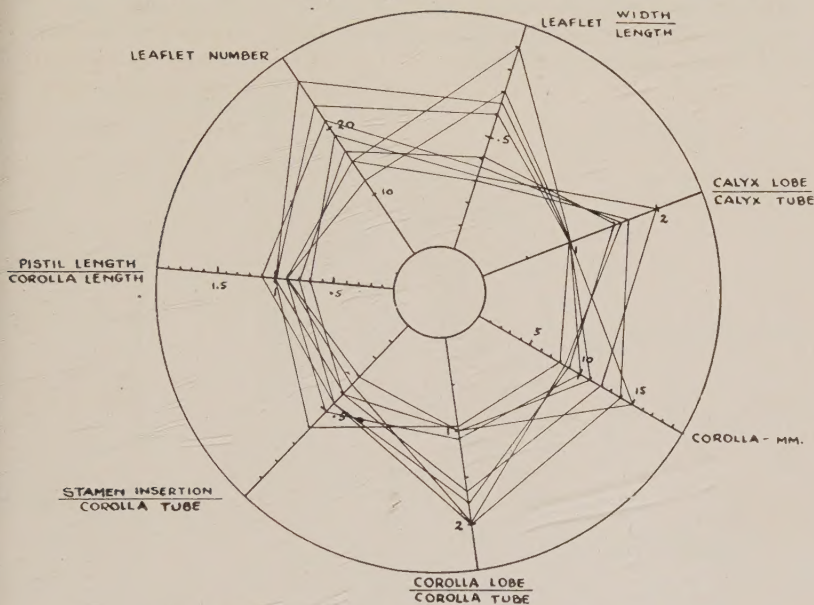
Fig. 3.   A mixed population has been graphed for seven characters. In the interest of simplicity only eight specimens are shown. The presence of two entities is demonstrated by the bimodal distribution on three of the radii. The other radii show normal distributions.

If all radii showed a normal distribution, similar to that of $\dfrac{\text{stamen insertion}}{\text{corolla tube}}$, other characters of possible diagnostic value would be selected. If these all showed normal distributions, the conclusion could be drawn that the population consisted of one variable entity.

mens may be compared on one base sheet. In larger populations, the use of thin paper or tracing paper makes superposition of two or more sheets possible, provided of course, that the same base measurement is retained. In some problems, particularly those dealing with the correlation of color with other characters, it may be expedient to use appropriately colored pencils to form the polygons.

After plotting a few members of a population, random variability is commonly apparent on some of the radii representing the selected characters. In practise it has been found convenient to

replace such characters with others, in order to test as many as possible for diagnostic value.

The completed figure will show a normal frequency distribution on any radius which represents a character which varies at random (fig. 3, corolla length, stamen insertion, pistil length). From such radii, the customary frequency curve may be constructed, if desired, by utilizing the number of specimens occurring in any desired interval.
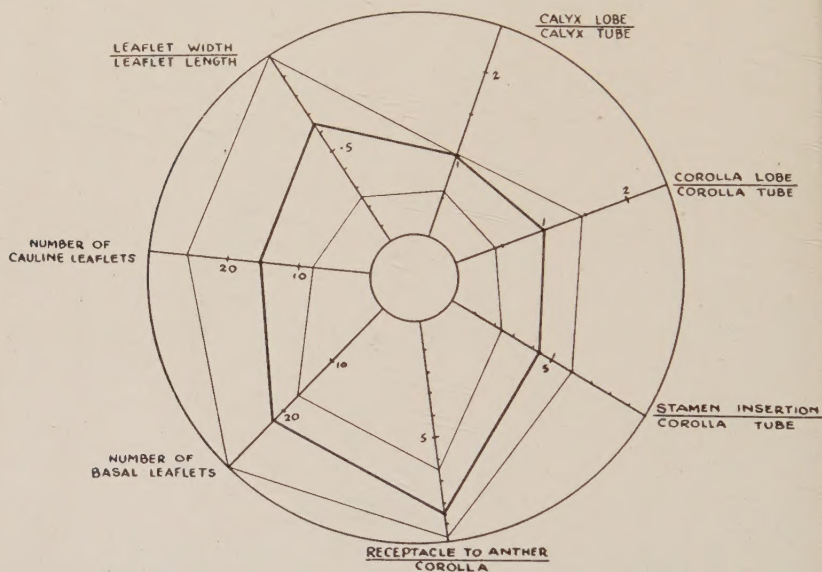
Fig. 4. A synopsis of a polygonal graph of a *Polemonium pulcherrimum* population from the Rocky Mountains of British Columbia and Montana. Compare the range of variation in each character in this population with the corresponding characters in the southern populations (figs. 5 and 6).

The occurrence of a bimodal distribution on any radius shows the presence of two entities, and if the distributions around each mode are mutually exclusive, the character would be valid for keying purposes. If several diagnostic characters have been graphed, the segregation into the two or more entities may be seen on the radius for each character (fig. 3, leaflet, calyx, and corolla proportions).

Positive correlation of characters is shown between adjacent radii by essentially parallel lines, as would be shown in figure 3, between calyx proportions and corolla proportions, were these two radii adjacent. Negative correlation is demonstrated in figure 3 between leaflet and calyx proportions, by the intersecting lines. The narrower leaflets show negative correlation with the

short calyx lobes, or conversely, positive correlation with the long calyx lobes. The fact that this correlation is not 100 per cent is shown in the specimen with the longest calyx lobe proportion. To show 100 per cent correlation, this specimen should have a leaflet proportion value of less than 0.3.

Figures 4, 5, and 6 show the use of the polygonal graph for
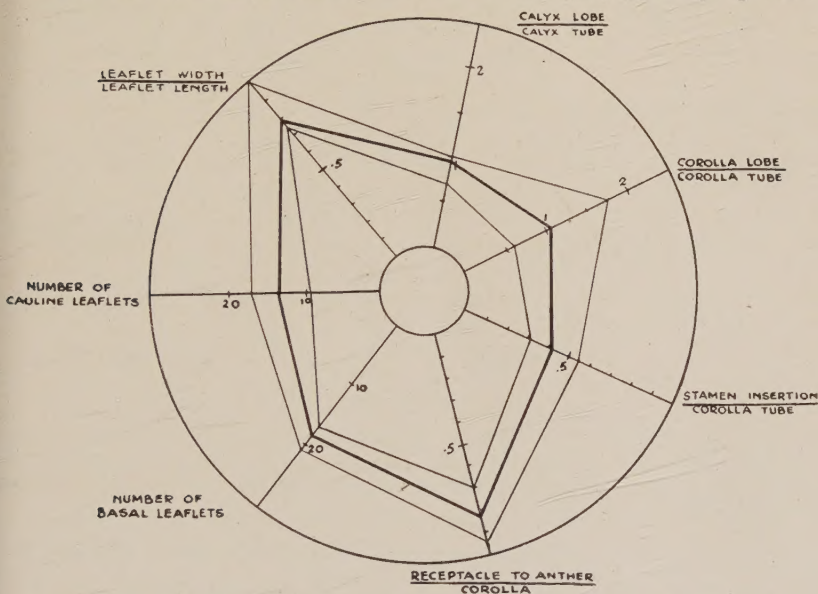
Fig. 5.   A synopsis of a *Polemonium* population from the Sierra Nevada of California which appears to be, on the basis of the graphed characters as well as other characters that were selected, a less variable form of *Polemonium pulcherrimum.*

the simultaneous comparison of seven characters in three distinct populations. In each figure, only the minimum, mean (heavy line) and maximum for each character has been plotted. The similarity of polygon shape in figures 4 and 5 is evidence of close relationship, considered here to be conspecific. Conversely, the difference in shape between figures 4 and 6 was the basis for rejection of conspecific status for these two entities. A further point shown in these figures is the reduced variability in both the southern populations as compared with the northern population.

The figures will serve to illustrate the method used, as well as to show some of the results obtainable.

LITERATURE CITED

HUTCHINSON, A. H. 1936. "The polygonal presentation of polyphase phenomena." Trans. Roy. Soc. Can., Ser. 3, Sect. V, 30: 19–26.
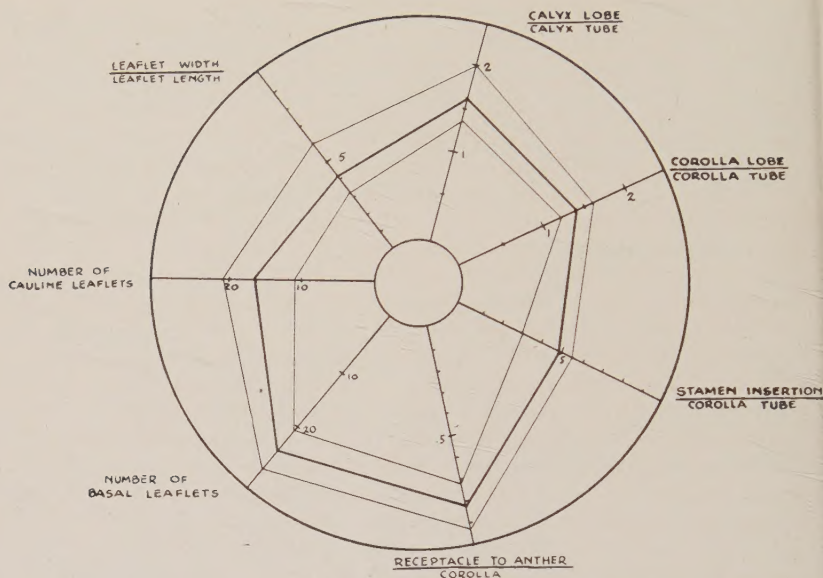
Fig. 6. A synopsis of another *Polemonium* population from the Sierra Nevada of California. The variation from *P. pulcherrimum* is evident in a number of respects in the mean (heavy line), but the calyx proportion appears to be most diagnostic.

————. 1940. Polygonal graphing of ecological data. Ecology 31: 475–487.

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MATURATION OF THE GAMETES AND FERTILIZATION IN NICOTIANA[1]

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Examination of megasporo- and megagametogenesis in a number of species of *Nicotiana* was undertaken with special reference to the extent to which details in the development of the female gametophyte might contribute evidence concerning species origins and relationships. The investigation was later extended to determination of the development, structure and behavior of the sperms. On this latter point no detailed reports have been published in the case of *Nicotiana* and relatively few references to megasporo- or megagametogenesis appear in the literature dealing with the genus.

For *N. tabacum* the complete sequence in megasporogenesis and embryo sac development was investigated with comparative studies, particularly of megagametogenesis, in a number of other species. In *N. alata* early stages were emphasized, in *N. sylvestris*, *N. glutinosa* and *N. rustica* 2- and 4-nucleate embryo sacs were studied while the character of the 8-nucleate condition in the same three species and in *N. rotundifolia* was compared. In addition, megasporogenesis in certain F_1 hybrids between more and less distantly related species was examined in comparison with that of the species above mentioned.

In *N. tabacum* the archesporial cell differentiating in the sub-epidermal layer of the nucellus at the apex of the ovule is initially distinguished by its large nucleus, deeply staining cytoplasm and, later, by its increase in volume as contrasted with the surrounding tissue. The archesporial cell becomes the megaspore mother cell directly, without division into parietal and sporogenous cells. Although in *N. tabacum* not more than one megaspore mother cell in an ovule has been seen, in *N. alata* twin megaspore mother cells (pl. 18, fig. 6), and later twin embryo sacs, each covered by its own nucellus, sometimes occur (cf. however, Satina, Blakeslee and Avery, 1934; Rees-Leonard, 1935; Cooper, 1943). In F_1 inter-specific hybrids more than one megaspore mother cell has often been observed and the same is true of chromosomal variants, par-ticularly of *N. tabacum,* derived from treatment of sporogenous or vegetative cells with high frequency radiation which, in addition, produced abnormalities in organization of nucellar and other tis-sues of the ovule.

At the time of differentiation of the megaspore mother cell in *N. tabacum* the ovule is erect but becomes completely anatropous at early meiotic stages. During this inversion epidermal cells at a level just below the lower end of the megaspore mother cell begin by periclinal divisions to form the single integument (pl. 18, fig. 1). It develops rapidly, two or three layers in thickness, and reaches the level of the apex of the nucellus before the end of pachytene, and almost completely covers it by diakinesis-MI (pl. 18, fig. 2).

During meiotic prophases the megaspore mother cell shows rapid increase in size, particularly in length (pl. 18, figs. 1, 2), while the cells of the nucellar covering become exceedingly nar-row and elongated (pl. 18, figs. 2–4). At the same time the inner-most layer of the integument begins differentiation to form the integumentary tapetum. The two meiotic divisions produce a quartet of megaspores—MII frequently occurring earlier in the chalazal than in the micropylar member of the dyad (pl. 18, fig. 4). More frequently the MII spindles are at right angles to each other producing a T-shaped quartet (pl. 18, fig. 3) although a linear quartet (pl. 18, fig. 4) is not uncommon. The chalazal megaspore becomes the 1-nucleate embryo sac and the other three megaspores soon degenerate (pl. 18, fig. 5).

In *N. tabacum,* therefore, the embryo sac is monosporic (cf. Maheshwari, 1941), as was also reported by Modilewski (1935). However, he found in *N. glauca* "a disporial eight-nucleate embryo sac according to the type of *Scilla,*" and in *Nicotiana ditagla* (amphidiploid *N. tabacum × N. glauca*) that "the monosporial process of formation of the embryo sac by means of forming a triad, occupies an intermediate position between the bisporial type which is proper to *N. glauca* and the monosporial type in form of a tetrad distinctive of [*N. tabacum*] Dubeck." In *N. rustica,* Persidski and Modilewski (1934) report that the development of the embryo sac "proceeds according to the disporial or *Scilla* type." Although complete analysis of the early sequence in *Nicotiana glauca* and *N. rustica* has not been made here, it is doubtful whether two distinct types of embryo sac development occur in a single genus. Furthermore, the illustrations and additional comments of the above named authors suggest that the two species in question are not typically bisporic.

Characteristic of the *Tubiflorae,* nucellar degeneration begins during the period of the extremely rapid growth in volume of the increasingly vacuolate 1-nucleate embryo sac while the remnants of the three non-functional megaspores are still present (pl. 18, fig. 5). This degeneration proceeds rapidly so that little indication of nucellar tissue is seen at the 2- and 4-nucleate stages, and almost none at the 8-nucleate stage (pl. 18, fig. 7).

Following the establishment of the 8-nucleate condition, one each of the four nuclei at the antipodal and at the micropylar end moves toward the center of the embryo sac. During this period the egg apparatus and the antipodal cells are matured. The former consists of triangular or pear-shaped synergids provided with basal vacuoles and a somewhat more spherical egg which continues to enlarge as a result of increase in size of an upper vacuole.

While in *N. tabacum* and *N. glutinosa* the mature embryo sac is pointed at the micropylar end and rounded at the chalazal end

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EXPLANATION OF THE FIGURES. PLATE 18

PLATE 18. SOME STAGES IN MEGASPOROGENESIS AND EMBRYO SAC FORMATION IN NICOTIANA. Figs. 1–4. Megasporogenesis in *Nicotiana tabacum.* Fig. 1. Megaspore mother cell, early prophase; origin of integument. Fig. 2. Same, diakinesis. Fig. 3. T-shaped quartet of megaspores. Fig. 4. Linear quartet; chalazal megaspores already formed, MII in upper dyad cell. Fig. 5. *N. tabacum.* 1-nucleate embryo sac; degeneration of other three megaspores advanced, of nucellus beginning. ×375. Fig. 6. *N. alata.* Twin nucelli, each with a megaspore mother cell. Fig. 7. *N. tabacum.* Mature embryo sac, normal organization of 8-nucleate condition, remnants of nucellus, chalazal end rounded. ×375. Fig. 8. *N. rotundifolia.* Same, chalazal end pocketed. ×375. Fig. 9. F₁ *N. tabacum × N. glauca.* Dyad degenerating; enlargement of cells of nucellar epidermis within integumentary tapetum (cf. fig. 4). All figures drawn with the camera lucida by a special carbon pencil technique from paraffin sections of ovules—longitudinal; reproduced ×290 unless otherwise indicated.

PLATE 18. SOME STAGES IN MEGASPOROGENESIS AND EMBRYO SAC FORMATION IN NICOTIANA.

(pl. 18, fig. 7), in *N. rustica* both ends are pointed; in *N. rotundifolia* (pl. 18, fig. 8)—to a lesser degree also in *N. sylvestris*—the chalazal end is distinctly pocketed. Although in the other species examined distinctions in the structure of the included cells serve to distinguish the two ends of the embryo sac, in *N. rotundifolia* two antipodals are similar to the synergids and the third antipodal suggests the egg. Attention is called to the fact that the species just referred to as differing in shape of embryo sac are members of three distinct taxonomic subdivisions of the genus. The extent to which such variations possess phylogenetic significance must, however, await further investigation.

Examination of megasporogenesis was made in a number of F_1 interspecific hybrids. In most cases the megaspore mother cell degenerates during meiosis, in some after the first and in others during the second division; the 4-megaspore stage was observed only in F_1 *N. bigelovii × N. suaveolens*. As degeneration proceeds the surrounding nucellar cells increase in volume (pl. 18, fig. 9) for a considerable period to produce a condition in striking contrast to that in species where, as already noted, the nucellar covering shows a progressive decrease in cell volume (cf. Greenleaf, 1941).

The sequence leading to the maturation of the female gametophyte, as summarized above, was determined from paraffin sections of *N. tabacum*[2] prepared by conventional techniques. Sections of entire ovaries from which the wall had been removed were cut at 15–20 μ and stained in iron haematoxylin. The following discussion of the origin, morphology and behavior in fertilization of the male gametes is based upon analysis of squash and smear preparations of *N. tabacum*[3] and of *N. longiflora* produced by a technique described elsewhere by Dr. Muriel V. Bradley (1948). By the use of this remarkably effective technique which permits examination of entire embryo sacs preceding and following fertilization many of the foregoing observations have been confirmed (cf., also, photomicrographs, Bradley, 1948).

In *Nicotiana* cytokinesis by furrowing originates the quartet of immature microspores which become the elliptical pollen grains. The mitosis producing the vegetative and generative nuclei is approximately central rather than near the wall of the microspore (Brumfield, 1941), apparently because of the absence of a central vacuole (Sax, 1935).

Normally in *Nicotiana* the division of the generative nucleus occurs in the pollen tube although under conditions of artificially induced germination this mitosis is sometimes observed in the pollen grain itself. Pollen tube mitoses have been studied in *N.*

[2] A variety collected, as an escape from cultivation, near Sartimbamba, northern Peru. The taxonomic status of other species referred to here is commented upon elsewhere (Goodspeed, 1945a).

[3] A variety collected, as an escape from cultivation, near Huaras, Peru.

tabacum, N. longiflora and *N. otophora*. Distinctions in chromosome morphology within the genoms of these species are clearly seen in these mitoses.   Thus, for example, in *N. otophora* the five long *st* and the seven short *m* chromosomes (Goodspeed, 1945b) can be distinguished (pl. 19, fig. 5).   Examination of pollen tubes of *N. tabacum* at increasing distances from the stigma indicates that the division of the generative nucleus characteristically occurs in the upper third of the style.

From dissections and smears of the stigma and style of *N. tabacum* it is clear that before pollen tube development the vegetative nucleus may exhibit marked alteration in form and substance.   At first, its outline becomes irregular and its contents somewhat diffuse and weakly staining (pl. 19, fig. 1).   Later, as it advances in the tube its substance is greatly extended.   As shown in plate 19, figure 3, its material becomes thrown into folds or loops and even, at times, a long, twisted ribbon commonly terminating, at one or both ends, in a more condensed region.   Its extension may be rather extraordinary (pl. 19, fig. 2).   Following

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EXPLANATION OF THE FIGURES.   PLATE 19

PLATE 19.   MATURATION OF THE MALE GAMETES AND FERTILIZATION IN NICO-TIANA.   Figs. 1–4, 6–16.   *N. tabacum,* n = 24; Fig. 5.   *N. otophora,* n = 12; Figs. 17–22.   *N. longiflora,* n = 10.   Fig. 1.   Pollen grain from stigma, early alteration in form of vegetative nucleus.   × 180.   Figs. 2–4.   Portions of pollen tubes from stylar canal.   × 290.   Fig. 2.   Extreme thread-like form of vegetative nucleus. Fig. 3.   More usual appearance of thread-like vegetative nucleus; late prophase of generative nucleus.   Fig. 4.   Later condensation of vegetative nucleus; anaphase of generative nucleus.   Fig. 5.   Division of generative nucleus in pollen tube, 5 large subterminal and 7 smaller median chromosomes.   × 850.   Fig. 6. Portion of pollen tube in micropyle; further condensation of vegetative nucleus (cf. figs. 2–4); sperms.   Figs. 7–22.   Studies of embryo sacs during and following fertilization (for details, cf. text).   Figs. 7–9.   Sperms, discharged from pollen tube, before contact with egg and larger fusion nucleus, sperms earlier elongated (figs. 7, 8), later spherical (fig. 9).   remnant of vegetative nucleus, tapering, pycnotic; degenerating nucleus of disrupted synergid ring-like; other synergid below pollen tube cytoplasm; sperm cytoplasm apparent (fig. 9). Figs. 10–12, 18, 19, 21.   Early, mid- and late fertilization stages, sperms undergoing alteration in form and structure; incorporation of sperm in fusion nucleus more rapid; tapering vegetative nucleus and one synergid pycnotic, other synergid intact; cytoplasm of early zygote differentiating (figs. 12, 21); cytoplasm of sperms apparent (fig. 11).   Figs. 13, 14.   Early and late fertilization, before fusion of polar nuclei; differentiation of zygote cytoplasm conspicuous. Fig. 15.   Entire embryo sac, late fertilization stage with incorporation of sperms almost complete; cellular character of antipodals.   Fig. 16.   Metaphase of first division of primary endosperm nucleus, *N. tabacum,* 72 chromosomes.   Fig. 17. Contents of two pollen tubes in embryo sac, post fertilization; sperms from second pollen tube near zygote and primary endosperm nucleus; pycnotic degeneration products of two vegetative nuclei (one above zygote) and two synergids.   Figs. 20, 22.   Post fertilization, persistence of vestiges of vegetative nucleus and one synergid nucleus, other synergid intact; differentiation of zygote cytoplasm; metaphase and telophase of first division of primary endosperm nucleus, *N. longiflora,* 30 chromosomes (fig. 20).   All figures drawn with the camera lucida by a special carbon pencil technique from squash or smear preparations; reproduced × 375 unless otherwise indicated.
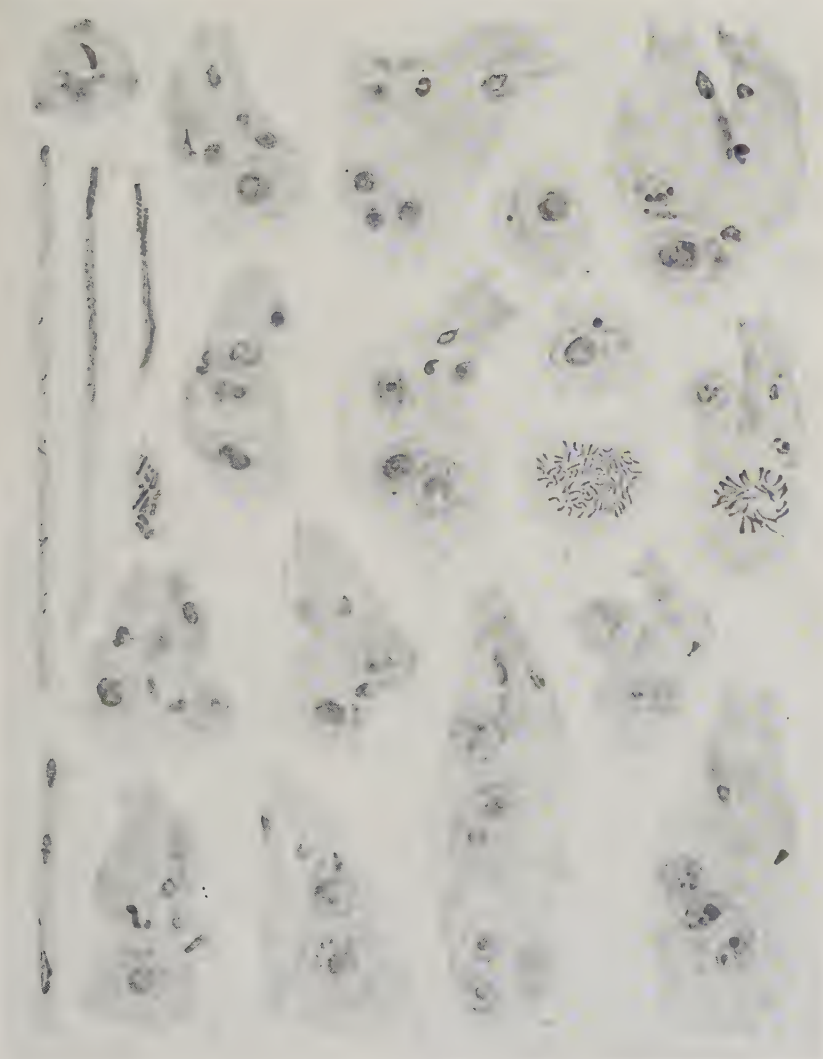
PLATE 19.   MATURATION OF THE MALE GAMETES AND FERTILIZATION IN NICOTIANA.

the division of the generative a certain condensation of the material of the vegetative nucleus occurs (pl. 19, fig. 4), which continues with increasing evidence of pycnosis as the tube enters the micropyle (pl. 19, fig. 6). A somewhat tailed, deeply staining structure represents an advanced stage in the degeneration of the vegetative nucleus. Variations in its appearance at fertilization and somewhat later are shown in plate 19, figures 7 to 15, and the fact that it persists at least until the primary endosperm nucleus is in division appears in plate 19, figures 20 and 22.

Numerous investigators (cf. Schnarf, 1941) have noted in other genera, and variously interpreted, similar changes in the form of the vegetative nucleus from the large, irregular, amoeboid, weakly staining condition characteristic of the pollen grain to the much extended, often almost thread-like form assumed in the tube. The change from an amoeboid to an extended form may be a response to protoplasmic streaming and the autonomous movement of the vegetative nucleus in the narrow confines of the tube (Tischler, 1925; O'Mara, 1933). Earlier literature attributes to the vegetative nucleus initiation of tube development followed by degeneration. More recent interpretations agree in questioning early degeneration and tentatively assign to the vegetative nucleus a function related to the continued growth of the tube (Schnarf, 1941; cf., however, Poddubnaja-Arnoldi, 1936). In *Nicotiana* degeneration as indicated by pycnosis is conspicuous only after growth of the pollen tube is at an end and, certainly, as suggested by Wulff (1933), if the vegetative nucleus is the bearer of growth-promoting substances any increase in its surface would have causal significance.

Studies of smears and squashes of styles and ovules of an horticultural race of diploid *Petunia* show, in this genus closely related to *Nicotiana,* a sequence of events in the development and degeneration of the vegetative nucleus corresponding to that in *Nicotiana.* However, in *Petunia* this nucleus is commonly more weakly staining and its irregularity and elongation are less conspicuous than in *Nicotiana.* Correspondingly, evidence of its degeneration is not conspicuous until after fertilization, by contrast with a strikingly pycnotic degeneration product of this nucleus which in *Nicotiana* is found along with the two sperms, in the tube cytoplasm previous to its contact with the female nuclei.

The proper squash technique applied to ovules provides an abundance of material for study of the sequence beginning with the penetration of the micropyle by the pollen tube and continuing through the divisions of the endosperm and zygote nuclei. Although the evidence thus obtained corresponds in general to that reported by Guignard (1902) for *N. tabacum,* a considerable amount of additional information is now available. Also, various stages in fertilization have for the first time been seen in species of *Nicotiana* other than *N. tabacum.*

Normally and as noted above, the 8-nucleate embryo sac of the species of *Nicotiana* investigated becomes the seven celled megagametophyte; the differentiation of synergids, egg and antipodals is accompanied by wall formation (cf. Bradley, 1948). Vacuolation produces a broad band of cytoplasm connecting egg, fusion nucleus and antipodals, with strands extending to the walls of the embryo sac. In at least one race of *N. tabacum* numerous deviations from such normal development occur (cf. Bradley, 1948; Persidski and Modilewski, 1934, in *N. rustica*). Thus, 9- to 16-nucleate embryo sacs have been seen, obviously the result of division of from one to all of the normal eight nuclei (cf., also, Korotkevich, 1940, in *N. rustica*). Frequently, alterations in normal position of nuclei, and particularly antipodal ones, occur. From one to three antipodals may wander to a position near the egg so that in some instances all nuclei are found in the micropylar end of the embryo sac (cf. Guignard, 1902).

Although polar fusion is usually complete before fertilization, it is in progress thereafter too frequently to be classed as an abnormality. Indeed, Guignard (1902) considered post fertilization fusion of the two polar nuclei normal behavior in *N. tabacum*. Fusion of three nuclei in 8-nucleate embryo sacs and of from three to five in the multinucleate embryo sacs above described has been observed. Twin embryo sacs have been found in squash preparations, with the corresponding nuclei similarly disposed and the two embryo sacs in identical stage of development.

In *N. longiflora,* and presumably in other species also, two pollen tubes may penetrate the micropyle. The contained cytoplasm of two tubes each with two sperms, a pycnotic vegetative nucleus and a degenerating synergid nucleus may be seen in contact with the female nuclei. On the other hand, penetration may not be simultaneous for, as shown in plate 19, figure 17, fertilization of both the egg (seen under the mass of tube cytoplasm) and fusion nucleus has apparently been effected by the sperms of the tube first penetrating the embryo sac while those of the second tube appear in the combined cytoplasm and presumably will later degenerate there.

In those species of *Nicotiana* studied the male gametes undergo little structural alteration from the time of their origin in the pollen tube until their contact with the female nuclei, and apparently the same is true of *Petunia*. Throughout they are somewhat elongated, ovoid bodies (pl. 19, figs. 6, 7; cf. Bradley, 1948, fig. 8). However, it is not possible to confirm the conclusions of Poddubnaja-Arnoldi (1936) and Sarana (1934) for *Nicotiana* nor the suggestion of Cooper (1946) for *Petunia* that the sperms in the pollen tube are cells. On the other hand, in both genera, and particularly in the latter, in squash preparations one sperm apparently within the egg cell and the other near or in contact with the fusion nucleus have been observed, each surrounded by a cyto-

plasmic accumulation limited by a membrane (pl. 19, figs. 9, 11), something quite distinct from the nimbus (frequently seen about other nuclei as well) interpreted by Guignard (1902) as a cyto-plasmic sheath but probably better interpreted as artefact.

The evidence both in *Nicotiana* and in *Petunia* of a cytoplasmic sheath about the sperms at the time of fertilization argues against the suggestion of Cooper (1946) that the x-bodies in the pollen tube of *Petunia* may represent remnants of cytoplasm originally surrounding and peculiar to the male gametes in the pollen tube. Apparently, in the two genera, structures interpreted as x-bodies by Cooper (1946) in *Petunia*—and perhaps also those interpreted as sperms by Ferguson (1927)—are actually remnants or de-generation products of vegetative and synergid nuclei (cf. also, Bradley, 1948).

In reports on fertilization in other genera the question whether the pollen tube discharges into a synergid or near it has been dis-cussed (Gerassimova, 1933; Warmke, 1943; Swamy, 1945). In *Nicotiana* just previous to fertilization a bulb-like protuberance of greater density than the cytoplasm of the embryo sac and con-taining the sperms and remnant of the vegetative nucleus is seen near or in contact with the egg and fusion nucleus. It may be interpreted as the swollen apex of the pollen tube after its impact has disrupted a synergid. On the other hand, it may represent a synergid into which the apical contents of the tube have been dis-charged (Guignard, 1902; Schnarf, 1941). At times, however, it appears that both the membrane of one synergid and that of the tube may have become ruptured at a point of contact, and that thereafter their combined contents may flow in bulb-like configu-ration deeper into the embryo sac. In any event, one synergid nucleus undergoes degeneration and is usually present in the cyto-plasm surrounding the sperms and remnant of the vegetative nucleus, while the second synergid commonly remains intact.

During fertilization the remnants of the vegetative and syner-gid nuclei are conspicuous. The former becomes increasingly pycnotic with its deeply staining material frequently tapering to produce a more or less extended, tail-like appendage (pl. 19, figs. 9, 11, 12) which is often dual or forked (pl. 19, fig. 15). In other cases—usually later stages—it is more contracted (pl. 19, figs. 10, 13, 14). At the same time the nucleus of the disrupted synergid also becomes pycnotic. It is distinguishable from the vegetative nucleus by form and position, usually appearing ring- or open ring-shaped and on a plane with the normal synergid (pl. 19, figs. 10–15, 20).

Although union of nuclei appears to follow almost immedi-ately upon the presence of the bulb-like mass of cytoplasm in the embryo sac, free sperms and the earliest stages of fertilization can be seen. The sperms are indistinguishable morphologically (pl. 19, figs. 6, 7, 9). At first somewhat elongated and oval, they

become spherical just previous to fertilization (pl. 19, fig. 9). In contact with the female nuclei they expand and become structurally more diffuse and loosely granular (pl. 19, figs. 10, 11) as they flatten against the nuclear membranes and gradually merge with the female nuclei along the lines of contact. Although initial contact of one sperm with the egg usually precedes that of the other sperm with the conspicuously larger fusion nucleus (cf. however, pl. 19, fig. 8), the fertilization process appears to be completed more rapidly in the latter case (pl. 19, fig. 12). Thus, the outline of the sperm nucleus with its included nucleolus is visible in the fertilized egg at a time when the only vestige of the sperm in the fusion nucleus is the presence of one or more small nucleoli in addition to the large nucleolus which, in the unfertilized fusion nucleus, represents the fusion product of the nucleoli of the polar nuclei (pl. 19, figs. 12, 14, 15, 18, 19). Indeed, the vestige of the sperm in the egg nucleus can be seen even after the division of the primary endosperm nucleus is in progress (pl. 19, figs. 20, 22). The egg cytoplasm undergoes a certain alteration in appearance which is sufficiently consistent as well as conspicuous to become diagnostic evidence that fertilization has occurred (cf. Schnarf, 1928). Before fertilization, the cytoplasm of the egg cell is concentrated at its base with a large vacuole occupying the micropylar end. After fertilization the egg cytoplasm appears to increase in volume, to be extended into the micropylar extremity of the cell and, in particular, to be denser and of a uniform consistency, becoming particulate or subdivided into more or less uniform aggregations, presumably by numerous small vacuoles (pl. 19, figs. 12, 14, 15, 20, 21, 22; cf. Bradley, 1948, fig. 9; cf. Schnarf, 1928).

Although post fertilization stages were not studied in detail it is clear that the first division of the zygote does not occur until after two or more divisions of the endosperm nuclei (cf. pl. 19, figs. 20, 22), as shown by the chromosome numbers involved (cf. pl. 19, figs. 16, 20).

Summary

The following features in megasporogenesis, megagametogenesis and fertilization in *Nicotiana* (with some comparative evidence in *Petunia*) are described and illustrated:

1. Distinctions in nucellar development and degeneration during embryo sac formation in species and F_1 interspecific hybrids; monosporic embryo sac.

2. Character of chalazal end of embryo sac in various species in relation to their taxonomic position.

3. Duplication of megaspore mother cells and embryo sacs; multinucleate embryo sacs; multiple pollen tubes.

4. Morphology of vegetative nucleus in pollen grain and tube; "x-bodies" as degeneration products of vegetative and synergid

nuclei; penetration of pollen tube via disruption of or discharge into a synergid.

5. Cellular character of sperms; their morphology before and their structural alteration during fertilization; alteration in cytoplasm of egg cell during and following fertilization; variations in time of polar fusion in relation to fertilization; rate of fertilization of egg and fusion nuclei and of subsequent development of zygote and endosperm.

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NOMENCLATORIAL CHANGES IN ELYMUS WITH A KEY TO THE CALIFORNIAN SPECIES

Frank W. Gould

In the preparation of a systematic treatment of the genus *Elymus* and the related *Agropyron, Sitanion,* and *Hystrix* groups for the "Manual of California Grasses" which Dr. Alan A. Beetle is preparing, the writer has been compelled by a considerable amount of evidence to view this complex of the Hordeae as a single genus. Previously proposed nomenclatorial combinations show that in the past other systematists have shared this concept at least partially. Admittedly there is still much to be learned concerning specific and subspecific relationships, but the evidence at hand indicates that the groups of species involved cannot be segregated satisfactorily on a generic plane. It is probable that further submergence of genera in the tribe Hordeae will result from current investigations, especially in the fields of cytogenetics and plant breeding. Fertile hybrid *Triticum* × *Agropyron* generations are reported by Veruschkine (1935) and Tzitzin (1936).

Linnaeus recognized five genera in the Hordeae complex, in the following order: *Lolium, Elymus, Secale, Hordeum,* and *Triticum.* He referred the two known species of *Agropyron* to *Triticum,* the one known species of *Hystrix* to *Elymus,* and indicated no disposition of the *Sitanion* group. Bentham and Hooker (1883) listed twelve genera in the Hordeae, treating *Agropyron, Triticum, Elymus,* and *Asperella* (*Hystrix*) as separate genera and including *Sitanion* as a section of *Elymus.* In North American grass treatments, Beal (1896), and Hitchcock (1935), follow essentially the Bentham and Hooker classification, but Hitchcock recognizes *Sitanion* as a genus distinct from *Elymus.*

Classically, *Elymus* and *Agropyron* are distinguished on the basis of the number of spikelets at each node of the rachis, the

former with two or more spikelets per node and the latter with one. This results in the rather arbitrary separation of species that are obviously closely related, as in the *Elymus triticoides, E. cinereus, E. condensatus, E. salina, Agropyron Smithii, A. arenicola* group, and the *Elymus glaucus, Agropyron subsecundum, A. pauciflorum* complex. The weakness of this basis for distinction is shown also by the following series of *Elymus* species in which the characteristic number of spikelets per node is: *E. salina,* one spikelet at a node; *E. triticoides* and *E. glaucus* two spikelets at a node but in forms of both species only one spikelet at a node; *E. cinereus* three spikelets at a node; *E. condensatus* eight or more spikelets at a node, counting those on pedicels.

It has been noted that in *Elymus* the florets are oriented more-or-less dorso-ventrally to the rachis while in *Agropyron* they are lateral. This tendency is recognized readily in some species but is not uniformly evident throughout the two groups. In some spikes of *E. triticoides* both conditions can be observed.

The type species of *Agropyron, A. triticeum* Gaertn., is an annual, very unlike the American agropyrons, all of which are perennial, and more similar to species of *Triticum.* This and the annual *Elymus caput-medusae* L., both sparingly introduced into North America from Europe, probably should be excluded from the genus *Elymus* as here interpreted.

Elymus and *Sitanion* probably have been treated more generally as sections of one genus than as separate genera. When retained as distinct they are separated on the basis of the readily disarticulating rachis and the usually narrow, setaceous glumes of the latter. If this distinction were followed rigidly, *Elymus aristatus,* as known in California, would appear more *Sitanion*-like than the classically recognized species *Sitanion Hansenii.*

Hystrix, a genus of about four species, has been split off from *Elymus* primarily on the basis of glume reduction, one or both being completely lacking in some cases. Plants of the North American species are very similar to species of *Elymus,* especially *E. interruptus* which also has irregularly reduced glumes.

Stebbins, Valencia, and Valencia in their recent papers on artificial and natural hybrids in the Hordeae (1946) present numerous points in agreement with the writer's independent conclusions. They give cytological evidence for assuming that *Elymus glaucus* and *Sitanion Hystrix* are even more closely related than some species of *Elymus* as previously delimited. They report the occurrence of *Elymus-Sitanion* and *Elymus-Agropyron* hybrids in nature and describe artificially produced *Sitanion-Agropyron* hybrids. Evidence is presented for the belief that all plants that can be classified as *Sitanion Hansenii* are sterile F_1 hybrids between *Elymus glaucus* and either *Sitanion Hystrix* or *Sitanion jubatum,* and that *Agropyron Saundersii* probably is composed of a series of F_1 hybrids between *Agropyron pauciflorum* and *Sitanion Hystrix* or

Sitanion jubatum. Reference is made to a colony of hybrid *Elymus glaucus* × *Agropyron pauciflorum* plants growing with the parent species near the Carnegie Institution experimental garden at Mather, Tuolumne County, California. This hybrid is discussed further by Hartung (1946).

The writer has noted an *Elymus* in the Sierra Ancha Mountains, Gila County, Arizona, which is morphologically intermediate between *Elymus glaucus* and *Agropyron subsecundum.* Plants of this type are abundant in the oak association at 5500 feet elevation, and no other forms of these two species occur in the vicinity.

ELYMUS L. Species Pl. 83. 1753. *Agropyron* Gaertn. Nov. Comm. Petrop. 14: 539. 1770. *Asperella* Willd. Roem. and Ust., Mag. Bot. 7: 5. 1790. *Hystrix* Moench. Meth. Pl. 295. 1794. *Sitanion* Raf. Journ. Phys. 89: 103. 1819. *Clinelymus* Griseb. Ledebour, Fl. Ross. 4: 330. 1853.

Annuals or perennials, many rhizomatous; blades linear or lanceolate, flat or involute, frequently glaucous, glabrous or variously pubescent; inflorescence basically spicate with 1 to 3 or occasionally 4 to 6 spikelets at a node, when more than 2 at one node one or more spikelets often short-pedicelled, in *E. condensatus* the inflorescence is a dense panicle; spikes disarticulating in the rachis or rachilla or both; glumes mostly subequal, reduced or absent in a few species, broadly lanceolate to attenuate or subulate, awnless, with a single principal awn, or with 2 to 4 awns or aristate teeth; lemmas mostly lanceolate, rounded on back, obtuse, acute, or aristate, usually inconspicuously nerved except near the apex; paleas mostly obtuse or truncate, about as long as and somewhat infolded by the lemmas.

Type species, *Elymus sibiricus* L. Species Pl. 83. 1753. (Concerning choice of type species see Hitchcock, 1936.)

KEY TO THE CALIFORNIAN SPECIES OF ELYMUS

**A. Lemmas awned, the awns mostly 1 to 3 cm. long;
plants typically without rhizomes**

Plants annual; lemma awns 3 to 8 cm. long; introduced weedy species .... 1. *E. caput-medusae.*
Plants perennial.
   Glumes absent or setaceous and scarcely reaching the first lemma .... 26. *E. californicus.*
   Glumes present and at least half as long as the first lemma.

I. Awns of lemmas curving outward at maturity

Rachis not disarticulating at maturity; internodes of spikes usually 1 cm. long or longer, the spikelets rather distant and distinct from each other; glumes mostly broad, acute or short-awned (occasionally long-awned in *E. arizonicus*).
Spikes with mostly 2 or 3 spikelets at a node ...... 12b. *E. glaucus* subsp. *Jepsonii.*

Spikes with mostly 1 spikelet at a node.
   Culms erect at base, usually 40 cm. long or longer;
     blades, at least some, longer than 10 cm.
      Culms slender; blades narrow, usually involute;
        spikes erect; spikelets usually closely ap-
        pressed; awns slender, sharply divergent   2. *E. spicatus.*
      Culms stout; blades 4 to 6 mm. or more broad,
        flat; spikes flexuous; spikelets usually
        spreading; awns stout, not sharply diver-
        gent ....   3. *E. arizonicus.*
   Culms usually decumbent at base, mostly 15 to 35
     cm. long; blades usually flat and short, 10 cm.
     or less long, mostly tufted at base of culms   4. *E. sierrus.*
Rachis readily disarticulating at maturity; internodes
   of spike usually 4 to 6 or 8 mm. long, the spikelets
   closely imbricated and rather crowded; glumes
   narrow, attenuate to setaceous, long-awned.
Spikelets mostly 1 at a node ....   5. *E. saxicolus.*
Spikelets mostly 2 at a node.
   Spikes, including awns, almost as broad as long;
     glumes bristle-like or cleft into bristle-like
     divisions, the body scarcely apparent.
     Glumes cleft into at least 3 divisions ....   6. *E. multisetus.*
     Glumes entire or 2-cleft ....   7. *E. elymoides.*
   Spikes much longer than broad; glumes lanceo-
     late, the body apparent ....   8. *E. Hansenii.*

*II. Awns of the lemmas straight or undulate, not curving
outward at maturity*

Spikelets mostly 1 at a node.
   Rachis readily disarticulating at maturity; glumes
     mostly attenuate, with awns 4 to 10 mm. long   9. *E. Saundersii.*
   Rachis not readily disarticulating; glumes acute or
     abruptly short-awned, the awns seldom over 4
     mm. long.
     Spikes relatively dense, the spikelets overlapping
       ½ to ⅔ their length; rachis internodes mostly
       4 to 8 mm. long .... 13a. *E. pauciflorus*
                                         subsp. *subsecundus*
     Spikes not dense, spikelets overlapping the one
       above on the opposite side of the rachis ¼ or
       less of their length; rachis internodes aver-
       aging 10 mm. or long.
       Culm nodes glabrous; lemmas usually long-
         awned; florets 3 to 5 per spikelet .... 13b. *E. pauciflorus*
                                         subsp. *laeve.*
       Culm nodes finely pubescent; lemmas short-
         awned; florets mostly 6 to 8 per spikelet 14. *E. Stebbinsii.*
Spikelets mostly 2 at a node.
   Rachis not disarticulating at maturity; glumes usu-
     ally broadly lanceolate, 3 to 5 nerved; culms
     usually in small clusters; common in California 12. *E. glaucus.*
   Rachis disarticulating at maturity; glumes narrowly
     lanceolate or subulate, 1 to 3 nerved; culms
     usually in dense clumps; rare or infrequent in
     California.
     Spikes slender, about 5 mm. broad, dense, the
       spikelets small, closely placed; lemmas 6 to 8
       mm. long excluding the awns; glumes lanceo-
       late, 1 to 3 nerved .... 11. *E. Macounii.*

Spikes stouter, mostly 8 to 10 mm. or more broad;
   lemmas 8 to 10 mm. long.
     Glume with awn mostly 1 to 1.5 cm. long; spikes
       usually 8 cm. or less long . . . .   10. *E. aristatus.*
     Glume with awn mostly 2.5 cm. long or longer;
       spikes usually more than 8 cm. long . . . . . .   8. *E. Hansenii.*

AA. Lemmas awnless or with awns 6 mm. or less long

Glumes broadly lanceolate, strongly 3 to 9 nerved,
   thin, or if thickened then the apex obtuse.
   Plants without rhizomes.
     Spikelets mostly 1 at a node.
       Culm nodes glabrous; florets 3 to 5 per spikelet . . 13. *E. pauciflorus*

       Culm nodes pubescent; florets mostly 6 to 8 per
         spikelet . . . . 14. *E. Stebbinsii.*
     Spikelets mostly 2 at a node . . . . 12a. *E. glaucus*
                                                           subsp. *virescens.*
   Plants with rhizomes.
     Spikelets mostly 1 at a node.
       Culm internodes 1 to 3 cm. long; rachis disar-
         ticulating at maturity; seashore . . . . 15. *E. multinodus.*
       Culm internodes mostly more than 4 cm. long;
         rachis not disarticulating.
         Lemmas glabrous or scabrous.
           Blades flat, thin and lax, bright green,
             rarely glaucous . . . . 18. *E. repens.*
           Blades usually involute, stiff, mostly glau-
             cous . . . . 20. *E. riparious*
         Lemmas finely pubescent . . . . 19. *E. subvillosus.*
     Spikelets mostly 2 at a node . . . . 16. *E. mollis.*
Glumes subulate, or if lanceolate then inconspicuously
   nerved, hard or tough in texture, and awn-tipped
   or acute.
   Spikelets mostly 2 to many at a node.
     Culms finely pubescent below the spike; glumes
       lanceolate; plants rhizomatous; seashore . . . . 17. *E. vancouverensis.*
     Culms glabrous below the inflorescence; glumes
       subulate or narrowly lanceolate.
       Spikelets 6 to 40 per node of the rachis includ-
         ing those on branches; culms usually 6 to
         10 mm. in diameter at base; blades 15 to 35
         cm. broad; coastal . . . . 24. *E. condensatus.*
       Spikelets 1 to 6 at a node, rarely more; culms
         usually less than 6 mm. in diameter; blades
         3 to 15 mm. broad.
         Culm nodes or vicinity of nodes with fine,
           usually dense pubescence; plants typi-
           cally non-rhizomatous . . . . 23. *E. cinereus.*
         Culm nodes glabrous; plants rhizomatous.
           Blades mostly 3 to 6 mm. broad; spikes
             with 1 or 2, occasionally 3, spikelets at
             a node; spikelets 8 to 15 mm. long with
             3 to 6 florets . . . . 22. *E. triticoides.*
           Blades mostly 6 to 15 mm. broad; at least
             some nodes of the spike with 3 to 6
             spikelets, or spikelets 17 to 25 mm. long
             and with 6 to 9 florets . . . . 22a. *E. triticoides*
                                                            subsp. *multiflorus.*

Spikelets mostly 1 at a node.
    Culms mostly 25 to 80 cm. long; spikes well ex-
        serted.
        Glumes narrow, usually awn-like; florets usually
            twisted so that the back of the lower lemma
            is centered between the glumes ....   22. *E. triticoides.*
        Glumes narrowly lanceolate but mostly broader
            than in *E. triticoides;* lowermost lemma of
            spikelet lateral to the rachis, the back not
            centered between the glumes ....   21. *E. Smithii.*
    Culms 10 to 20 cm. long; spikes little exserted,
        often exceeded by the blades; seashore ......   25. *E. pacificus.*

The following species of Elymus occur in California.
1. Elymus caput-medusae L. Sp. Pl. 84. 1753.

2. **Elymus spicatus** (Pursh) comb. nov. *Festuca spicata* Pursh,
Fl. Am. Sept. 83. 1814. *Agropyron spicatum* Scribn. & Smith, Bull.
U. S. Div. Agrost. 4: 33. 1897.

3. **Elymus arizonicus** (Scribn. & Smith) comb nov. *Agro-
pyron arizonicum* Scribn. & Smith, Bull. U. S. Div. Agrost. 4: 27.
1897. *A. spicatum* var. *arizonicum* M. E. Jones, Contr. West. Bot.
14: 19. 1912.

4. **Elymus sierrus** nom. nov. *Agropyron Gmelini* var. *Pringlei*
Scribn. & Smith, Bull. U. S. Div. Agrost. 4: 31. 1897. *A. Pringlei*
Hitchcock ex Jepson, Fl. Calif. 1: 183. 1912. Not *Elymus Pringlei*
Scribn. & Merr., 1901.

5. Elymus saxicolus Scribn. & Smith, Bull. U. S. Div. Agrost.
11: 56. 1898. *Sitanion flexuosum* Piper, Erythea 7: 99. 1899.
S. lanceolatum J. G. Smith, Bull. U. S. Div. Agrost. 18: 20. 1899.
Agropyron saxicola Piper, Contr. U. S. Nat. Herb. 11: 148. 1906.

6. Elymus multisetus (J. G. Smith) Davy, Univ. Calif. Publ.
Bot. 1: 57. 1902. *Sitanion jubatum* J. G. Smith, Bull. U. S. Div.
Agrost. 18: 10. 1899. Not *Elymus jubatus* Link, 1827. *Sitanion
multisetum* J. G. Smith, Bull. U. S. Div. Agrost. 18: 11. 1899.

7. Elymus elymoides (Raf.) Swezey, Nebr. Pl. 15. 1891.
Aegilops Hystrix Nutt., Gen. Pl. 1: 86. 1818. Not *Elymus Hystrix*
L. 1753. *Sitanion elymoides* Raf., Jour. Phys. 89: 103. 1819.
Elymus Sitanion Schult., Mant. 2: 426. 1824. *Sitanion Hystrix*
J. G. Smith, Bull. U. S. Div. Agrost. 18: 15, pl. 2. 1899.

8. Elymus Hansenii Scribn., Bull. U. S. Div. Agrost. 11: 56,
fig. 12. 1898. *Sitanion Hansenii* J. G. Smith, Bull. U. S. Div.
Agrost. 18: 20. 1899.

9. Elymus Saundersii Vasey, Bull. Torrey Bot. Club 11: 126.
1884. *Agropyron Saundersii* Hitchcock, Proc. Biol. Soc. Wash. 41:
159. 1928. *Elymus Saundersii* var. *californicus* Hoover, Leafl. West.
Bot. 3: 254. 1943.

10. Elymus aristatus Merrill, Rhodora 4: 147. 1902. *F glaucus aristatus* Hitchcock ex Abrams, Illus. Fl. Pacific States 1 252. 1923.

11. Elymus Macounii Vasey, Bull. Torrey Bot. Club 13: 119 1886. *Terellia Macounii* Lunell, Am. Midl. Nat. 4: 228. 1915.

12. Elymus glaucus Buckley, Proc. Acad. Nat. Sci. Phila 1862: 99. 1862. *Clinelymus glaucus* Nevski, Bull. Jard. Bot. Acad Sci. U. R. S . S. 30: 648. 1932.

12a. E. glaucus Buckley subsp. virescens (Piper) comb. nov *E. virescens* Piper, Erythea 7: 101. 1899.

12b. E. glaucus Buckley subsp. Jepsonii (Davy) comb. nov *E. glaucus* var. *Jepsonii* Davy ex Jepson, Fl. West. Mid. Calif. 79 1901. *E. glaucus* f. *Jepsonii* St. John, Fl. S. E. Wash. & Adj Idaho 42. 1937.

13. Elymus pauciflorus (Schwein.) comb. nov. *Triticum pauc florum* Schwein., in Keating, Narr. Exped. Winnipeg 2: 383. 182 *T. trachycaulum* Link, Hort. Berol. 2: 189. 1833. *Agropyr tenerum* Vasey, Bot. Gaz. 10: 258. 1885. *A. pauciflorum* Hitchcoc Am. Jour. Bot. 21: 132. 1934.

13a. E. pauciflorus (Schwein.) Gould subsp. subsecundu (Link) comb. nov. *Triticum subsecundus* Link, Hort. Berol. 2 190. 1833. *T. Richardsoni* Schrad. Linnaea 12: 467. 1838. *Agr pyron subsecundum* Hitchcock, Am. Jour. Bot. 21: 131. 1934.

13b. E. pauciflorus (Schwein) Gould subsp. laeve (Scribn. Smith) comb. nov. *Agropyron Parishii* Scribn. & Smith var. *laev* Scribn. Smith, Bull. U. S. Div. Agrost. 4: 28. 1897. *A. laev* Hitchcock ex Jepson, Fl. Calif. 1: 181. 1912.

14. Elymus Stebbinsii nom. nov. *Agropyron Parishii* Scrib & Smith, Bull. U. S. Div. Agrost. 4: 28. 1897. Not *Elymus Parish* Davy & Merrill, 1902.

This species is named in honor of Dr. G. Ledyard Stebbins, J of the University of California. For the past several years D Stebbins has made cytogenetical investigations of species of th Hordeae tribe, and has contributed substantially to our knowledg of phylogenetic relationships in this group. Dr. Stebbins ha worked specifically with the *Elymus* complex to which the speci named in his honor belongs.

15. Elymus multinodus nom. nov. *Triticum junceum* L., Man Pl. 2: 327. 1771. Not *Elymus junceus* Fisch. 1811. *Agropyr junceum* Beauv., Ess. Agrost. 102. 1812.

16. Elymus mollis Trin. ex Spreng., Neue Entdeck. 2: 7 1821.

17. Elymus vancouverensis Vasey, Bull. Torrey Bot. Club 1 48. 1888.

18. **Elymus repens** (L.) comb. nov. *Triticum repens* L. Sp. Pl. 86. 1753. *Agropyron repens* Beauv., Ess. Agrost. 102. 1812.

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TWO NEW VARIETIES OF CONDALIA FROM TEXAS

V. L. Cory

The small pasture, or horse trap, in which the horses are grazed at the Texas Agricultural Experiment Station, Substation No. 14, contains 118 acres. The pasture is at the summit of the Edwards Plateau at an elevation of 2400 feet, and has a surface comparatively level except for the heads of two small drainage courses. A gently rounded, highly calcareous knoll in the south-central portion of the pasture covers several acres and bears an almost pure stand of *Juniperus Pinchoti* Sudw. with a slight admixture of *Quercus Vaseyana* Buckl. Below the knoll on the west occurs a variety of shrubby vegetation; farther on, in the upper part of a little valley, the shrubs give way to grassland. In this shrubby vegetation occur four kinds of *Condalia,* all growing within twenty-five feet of each other, a circumstance which I do not recall having observed elsewhere. One of these forms of *Condalia* occurs as a close colony and appears to merit varietal recognition.

Condalia obovata Hook. var. **edwardsiana** var. nov. A specie differt foliis longioribus angustioribusque, spatulatis nec obovatis. This differs from the typical form of the species in its longer and narrower leaves, which are spatulate instead of obovate.

Type. Twenty-nine airline miles northwest of Rocksprings, Edwards County, Texas, altitude approximately 2400 feet, May 27, 1943, *Cory 41784* (Arnold Arboretum, Harvard University).

This variety is markedly different in appearance from other members of the genus in this area because of its greater height and lighter-colored foliage. Even after long and diligent search, I have been unable to find it anywhere save in this single, isolated thicket. It is closely related to the typical phase of the species, which inhabits the Rio Grande Plains of Texas and northern Mexico, but does not reach the Edwards Plateau or even the escarpment area.

The colony of *Condalia obovata* var. *edwardsiana* is essentially a pure consociation. The thicket is irregularly ovate, with a long diameter of 45 feet and a short diameter of 30 feet, comprising a calculated area of 900 square feet. It contains about 100 trunks, or 20 to 25 individual plants. The tallest is 3.1 meters high, and the average height is about 2.5 meters. Along the margins of this pure stand occur the following woody plants: *Quercus virginiana, Berberis trifoliata, Rhus microphylla, R. virens, Prosopis juliflora glandulosa, Diospyros texana, Opuntia leptocaulis, Cissus incisa, Colubrina texensis,* and *Condalia obtusifolia.* A plant of *Condalia viridis* Johnston is growing twenty feet south of the west end of the thicket, and there are a few others nearby on the south and west, some of them in thickets of *C. spathulata* Gray. Twenty-two feet southwest of the southwest corner of the pure stand of *C. obovata* var. *edwardsiana* is the nearest plant of *C. spathulata,* a species which is abundant southwest of this area. There are two plants of *C. obtusifolia* at the southwestern margin of the consociation. The plants of *C. viridis* and *C. obtusifolia* are clearly distinguishable from those of *C. spathulata* by their greater height. On May 27, 1943, only *C. obtusifolia* showed any stage of inflorescence, and it presented all the stages from bud to mature fruit, frequently on a single branchlet. The fruit of *C. obtusifolia,* which is much larger than that of the other condalias, changes from green to reddish and finally to an intense bluish-black upon maturing.

In 1937, Mr. Hiram Reed, a former associate of mine in the United States Department of Agriculture, retired and came to Sonora, Texas, to live. He retained his interest in plants, particularly those of some economic significance, and from time to time turned his collections over to me. Among the first lot of these collections was a *Condalia* from the hills of the Garner State Park in northern Uvalde County, Texas. At first, this specimen was referred to *C. obovata,* but subsequent detailed field study, especially on *C. obovata* and on *C. viridis* showed that it was more closely related to the latter species. In my field experience, I found that *C. obovata* is of common occurrence from sea level up to the base of the Escarpment of the Edwards Plateau, or up to elevations of approximately 600 feet, while *C. viridis* is common on the Edwards Plateau and west and south of that area at elevations of 2000 feet or more. In between these two elevations, and occupying the Escarpment area of the Edwards Plateau, is the plant under discussion. I wish to dedicate this newly recognized variety to the man who first called it to my attention, to my friend of former days as well as of the present, Mr. Hiram R. Reed.

CONDALIA VIRIDIS Jtn. var. **Reedii** var. nov. A specie differt vulgo statura duplo majore foliisque duplo majoribus (i.e., ad 13 mm. longis, 6 mm. latis).

This variety differs from the species in being (on the average)

twice as tall with at least twice its spread, and with leaves about twice as large, or up to 13 mm. long and 6 mm. broad.

Type.   Northeastern or eastern brow of hills along the Frio River, Garner State Park, Uvalde County, Texas, altitude 1500 to 1600 feet, June 4, 1944, *Cory 44496* (Arnold Arboretum, Harvard University).

I know of this variety only in the Escarpment Area of the Edwards Plateau at elevations below 2000 feet.   It is my opinion that two of the specimens cited by Johnston for his species, *C. viridis* (*Palmer 164,* Eagle Pass, Val Verde County, 1880, and *Harvard 61,* Eagle Pass, 1882), should instead be referred to var. *Reedii.*   Eagle Pass in on the Rio Grande in Maverick County; the highest elevation in Maverick County is 956 feet.

Rather commonly, on account of its obovate leaves, var. *Reedii* has been confused with *C. obovata,* which it does resemble in its growth and general appearance.   The light-green foliage of *C. obovata,* however, serves to separate it at once from var. *Reedii* and our other species of *Condalia.*   On the other hand, *C. viridis* typically in the field might be easily confused with *C. obtusifolia* but never with *C. obovata.*

CONDALIA OBTUSIFOLIA (Hook.) Weberb.   *R(hamnus*) ? *obtusifolia* Hook. ex Torr. & Gray, Fl. N. Am. 1 : 685. 1840.   *Zizyphus obtusifolia* (Hook. ex Torr. & Gray) A. Gray, Genera 2 : 170. 1849. *Condalia obtusifolia* (Hook.) Weberb. in Engler & Prantl, Pflanzenf. 3 : 404. 1850.   *Zizyphus lycioides* A. Gray, Boston Jour. Nat. Hist. 6 : 168. 1850.   *Condalia lycioides* (A. Gray) Weberb. in Engler & Prantl, Pflanzenf. 3 : 404. 1850.

For twenty years I have searched unsuccessfully for the entities described as *Condalia obtusifolia* (Hook.) Weberb. and *C. lycioides* (A. Gray) Weberb., and I have finally reached the conclusions that the two are synonymous.   At my request, Dr. Ivar Tidestrom checked the material of these two alleged species at the United States National Museum and agreed with the above disposition of *C. lycioides.*   In young growth or in new growth of old plants the foliage is typically that of *C. obtusifolia,* and very frequently the young growth contrasts markedly with the more abundant older growth of the same plant which has foliage typically that of *C. lycioides.*   A plant with the linear, oblong, or elliptic leaves characteristic of *C. lycioides* will, upon being cut off at the surface of the ground, send up vigorous sprouts with orbicular leaves as much as 2 cm. in diameter.   At and toward the eastern limit of its range in Texas the plant more commonly has foliage typical of *C. obtusifolia,* while a few hundred miles farther west, the more common type of foliage is that of *C. lycioides.*   Complete intergradation of the two extremes, however, is evidence of their conspecifity. Specimens verifying this conclusion have been deposited at the Arnold Arboretum, Harvard University.   The common species of

Condalia occurring from central Texas westward to southern California and south into northern Mexico should be known, therefore, as *Condalia obtusifolia* (Hook.) Weberb.

I am indebted to Dr. I. M. Johnston and to Mr. Ernest J. Palmer for critical study of material and for suggestions as to treatment, to Dr. Lloyd Shinners for valuable assistance with the Latin diagnoses, and to Dr. Bassett Maguire for the above synonymy.

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A NEW VIOLET FROM MEXICO

Milo S. Baker

Viola galeanaensis sp. nov.   Geophytum perspicuum, foliis partibusque caulis tandrum supra solum; glabrum praeter granulis dispersis superficierum superiarum venarum mediarum propeque ad marginibus aliquot foliorum; rhizoma erecta, 2–4 cm. longa, multis radiculis crassis; petioli foliorum radicitorum usque ad 8 cm. longi, foliorum caudicitorum breviores sed semper plures longitudines laminae folii multiplicata, laminae late ovatae, ad basim tenuiter cordatae, apiculatae, leviter crenatae, prope longiores quam latiores, usque ad 18 mm. longae; stipulae oblongae-lanceolatae, prope integrae, scariosae, usque ad 9 mm. longae; caulis 1–3, fere subterraneae, 2–5 mm. longae; flores axillares, 9–13 mm. longitudinibus; peduncula 3–5 cm. longi, bracteolae filiformes, propinquae ad florem; sepala 4–5 mm., inferiori fere maiores, lanceolati, marginibus scariosis, acuti, auriculae parvae, rotunditatae; corolla pallida purpurea usque ad alba, pars media flava nervis et dorso atris, petala laterales leviter clavata-barbati, calcar brevissimum; vagina staminis apertione-collare angusto; stylus vix 2 mm. longus, abrupte inflectus prope ab ovario, abrupte amplificatus ad caput clavatum, leviter barbatus ad lateribus, stigma rostrum minimum ad superficiem ventralem capitis; capsula globosa, glabra, semina incognita.

A pronounced geophyte with only leaves and parts of the stems above the soil; glabrous except for scattered granulations along the upper surface of the midveins and near the margins of some leaves; rootstock erect, 2 to 4 cm. long, with many coarse roots; petioles of radical leaves up to 8 cm. long, those of cauline leaves shorter but always several times length of blade, leaf blades broadly ovate, shallowly cordate at base, apiculate, remotely serrate, approximately as wide as long, up to 18 mm. long; stipules oblong-lanceolate, nearly entire, scarious, up to 9 mm. long; stems 1 to 3 mostly subterranean, 2 to 5 cm. long: flowers axillary 9 to 13 mm. in length; peduncles 3 to 5 cm. long, bractlets filiform, near the flower; sepals 4 to 5 mm., the lower ones much larger,

lanceolate, scarious margined, acute, auricles small, rounded; corolla pale lilac to white with yellow center with purple veins and back, lateral petals lightly clavate-bearded, spur very short; stamen sheath with narrow collar-opening; style scarcely 2 mm. long sharply bent near ovary, abruptly widened into a clavate-head, lightly bearded on the sides, the stigma a minute beak on the ventral surface of head: capsule spherical, glabrous, seeds unknown.

Type. Near the peak of Cerro Potosi, 11,900 feet, Municipio de Galeana, Nuevo Leon, Mexico, 1938, *Mexican Biological Expedition of Students of the University of Illinois, 923* (Gray Herbarium). A specimen in the United States National Herbarium labelled only Cerro Potosi, Nuevo Leon, Mexico, *R. Schneider 923,* is doubtless an isotype.

Other collections. Altitude 9,000–10,000 feet, Mount Infernillo, 15 miles southwest of Galeana: common on peak, June 16, 1934, *C. H.* and *M. T. Mueller 828* (Gray Herbarium), June 29, 1934, *F. W. Pennell 17126* (United States National Herbarium).

Character	*V. galeanaensis*	*V. flagelliformis*	*V. pedunculata*
Rootstock	more or less erect, but deep-seated with many coarse roots	more or less erect, not deeply buried; same type of roots	erect or horizontal, often as wide as long, buried 10 to 15 cm.; numerous coarse roots
Stems	one-half subterranean; decumbent to erect	not at all or only slightly subterranean; weak, decumbent to trailing	one- to two-thirds subterranean; erect to decumbent; never weak and trailing
Height including rootstock	up to 11 cm.	up to 50 cm.	up to 25 cm.
Width	up to 10 cm.	up to 22 cm.	up to 38 cm.
Pubescence	glabrous throughout	conspicuously hirsute throughout except glabrous seed pods	microscopically puberulent except glabrous seed pods
Leaves	broadly ovate, shallowly cordate, remotely and faintly serrate; thick	reniform to broadly ovate, deeply cordate, regularly and conspicuously serrate; not conspicuously thickened	ovate, subcordate to truncate, serration irregular and remote; thick
Stipules	small and scarious	small, thin, green	much larger, green
Flower	small, pale lavender or white, with yellow center	small, yellow	large, orange
Pistil	Chamaemelanium type	Chamaemelanium type	Chamaemelanium type
Life-Zone	Upper Sonoran to Transition ?	Lower Sonoran	Upper Sonoran

This violet is of interest to botanists of California because of its affinity to *Viola pedunculata* T. & G.   Although *V. pedunculata* is a very much larger plant than *V. galeanaensis,* and its large yellow flowers present a very different appearance, yet in vital characters, as shown in the table below, these two species are much alike. The closest relative of *V. galeanaensis* is unquestionably the Mexican species *V. flagelliformis* Hemsley, from which it is doubtless derived.   However, the characters of *V. galeanaensis* suggest that it may be the original progenitor of the far distant Pacific Coast species, *V. pedunculata* T. & G.   The principal characters of these three species are summarized in the above table.

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</div>

A NEW SPECIES OF OXYTROPIS FROM THE CENTRAL ROCKY MOUNTAINS

C. L. PORTER

Oxytropis obnapiformis sp. nov.   Subscaposis, sericeis, argenteis, erectis, perennis, 1–3 dm. altitudine; foliis pinnatis, 11–25-foliolatis, foliolis oblongo-lanceolatis, 5–30 mm. longitudine, 2–4 mm. latitudine; stipulis adnatis petiolis; scapis foliis subaequalibus vel longioribus, ca. 10–20 floris; corollis purpurascentibus, 15–20 mm. longis, leguminibus ovatis, inflatis, ad rostrum vehementer contractis, villosis albis, subcoriaceis, basi ad rostrum 8–12 mm. longa, 5–8 mm. lata, rostrum 5–8 mm. longum, sectione transversa cordata, sutura superiore introflexa fere ad medium; semina complura, reniforma, 1–2 mm. longa.

Grayish strigose or villous subscapose erect perennials, 1–3 dm. high, from a silky multicipital caudex surmounting a slender taproot; leaves pinnate, mostly 11–25-foliolate, the leaflets oblong-lanceolate, 5–30 mm. long, 2–4 mm. wide, grayish with somewhat appressed silky pubescence; stipules adnate to the petiole, scarious and villous-pubescent; scapes equaling or exceeding the leaves, about 10–20-flowered, the inflorescence a spicate raceme; bracts about 5 mm. long, lanceolate; calyx cylindrical at time of blooming, about 10 mm. long, grayish-strigose or villous, the teeth lanceolate to oblong, 2–3 mm. long; corolla purplish, the banner pale to white in the center with purple margin, 15–20 mm. long; mature fruit splitting the calyx and exserted, ovoid and inflated, with an abrupt slender beak, softly white-villous, somewhat transversely wrinkled when dry, the texture thin-coriaceous, the body 8–12 mm. long, 5–8 mm. broad, the beak 5–8 mm. long, the cross section cordate in outline with the ventral suture intruded about to the middle; seeds several in each pod, reniform, 1–2 mm. long.

Type.   Sand hills 8–9 miles west of Maybell, on U.S. 40, elevation 5,900 ft., Moffat County, Colorado, *Porter 3864,* June

19, 1946 (Rocky Mountain Herbarium, University of Wyoming,
Laramie. Isotypes, Gray Herbarium, Harvard University; United
States National Museum; New York Botanical Garden; Missouri
Botanical Garden; Colorado Agricultural & Mechanical College;
University of California; and herbarium of R. C. Barneby, Wap-
pingers Falls, New York).

Cotypes. From type locality, July 6, 1945, *Porter 3616* (Rocky
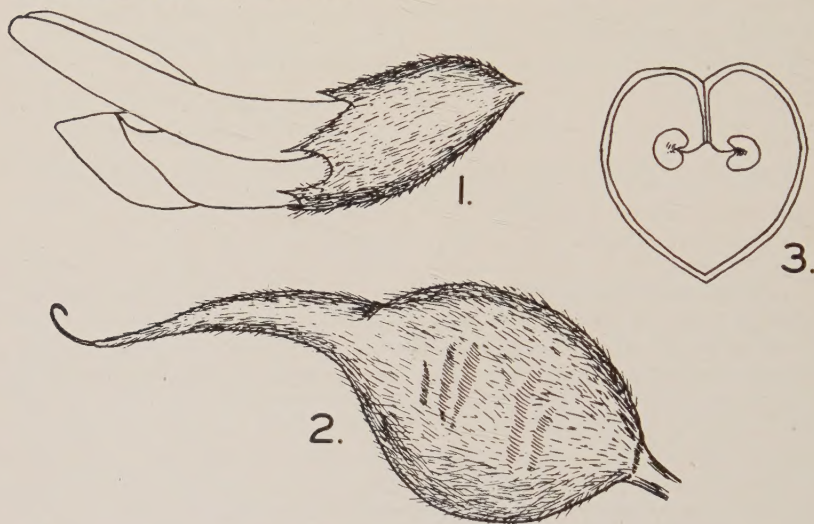Mountain Herbarium, Gray Herbarium, New York Botanical

Fig. 1. *Oxytropis obnapiformis* Porter: *1*, flower with wing removed;
2, fruit; *3*, cross section of fruit. All approximately × 3.75.

Garden, Philadelphia Academy of Sciences, University of Wash-
ington, University of Texas, and Southern Methodist University);
from type locality, June 19, 1946, *Harrington 1906* (Colorado
Agricultural & Mechanical College); from dry rocky hillsides
near Five Springs Falls, elevation 7,500 ft., Big Horn County,
Wyoming, July 11, 1936, *Williams & Williams 3314* (Rocky Moun-
tain Herbarium); from the mouth of Shell Canyon, elevation 4350
ft., Big Horn County, Wyoming, *Ripley & Barneby 8010* (Rocky
Mountain Herbarium, and the herbarium of R. C. Barneby).

This interesting species, common to the western slope of the
Big Horn Mountains of Wyoming and the dry sandy hills of north-
western Colorado, is named in allusion to the somewhat inverted
turnip-shaped pods, these being its most unique distinguishing
feature. It is undoubtedly a member of the section *Campestres*,
and in foliage and flower characteristics closely resembles mem-
bers of the *O. Lambertii* complex. It blooms early in June or even
in May in the type locality, since it was well past most of its

blooming period when collected June 19, only a few flowers re-
maining on occasional plants. The specimen collected by Wil-
liams has both flowers and mature fruit; that collected by Barneby
has only fruits. The plants from Wyoming appear to have a
tendency toward a more exserted inflorescence than those from
Colorado, but this may be due to a habitat difference since there
is little else to distinguish them.

The writer is indebted to Mr. R. C. Barneby for making his
collection available for study, thus adding to our knowledge of
the known range of the species.

Department of Botany and
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(Contribution No. 203).

REVIEW

Los Juniperus Mexicanos. By Maximino Martínez. Tom 17,
Anales del Instituto de Biologia de la Universidad Nacional de
Mexico, Mexico, D. F., 1946. 128 pp., 108 figs., paper cover.

A few months ago, in reviewing Professor Martínez's book on
the genus *Pinus* in Mexico, I expressed the hope that he would
continue to produce papers of comparable excellence. In issuing
the above paper on the genus *Juniperus* in Mexico he has fulfilled
that hope.

The first twenty-four pages of the paper are utilized in dis-
cussing the general characteristics of the genus and its representa-
tives in Mexico; a few paragraphs on the qualities of the lumber
produced by Mexican junipers; the vegetational zones in different
parts of the country; the subgeneric classification; and several
lists of species and lower entities based on such characters as size
of fruit, number of seeds and nature of the bark. This is followed
by a key to the species and full descriptions of the entities recog-
nized, together with citations of references and specimens ex-
amined.

Prior to 1944 only four species of *Juniperus* had been recog-
nized as occurring in Mexico. In this paper Professor Martínez
accepts twelve species, six varieties, and three formas. All of these
fit into Spach's section *Sabina,* and Martínez has distributed them
among five subsections, the *Flaccidae, Deppeanae, Jaliscanae, Monti-
colae* and *Monospermae.* Of this number, four species (*J. jaliscana,
Blancoi, durangensis,* and *Patoniana*) ; six varieties (*J. jaliscana* var.
typica and var. *poblana, J. Deppeana* var. *robusta* and var. *zacatecen-
sis, J. monosperma* var. *gracilis,* and *J. erythrocarpa* var. *coahuilensis*) ;
and three formas (*J. Patoniana* forma *obscura, J. monticola* forma
compactum and *J. monticola* forma *orizabensis*) are described as
new. One new combination and one new name also are proposed.
Two other species, *J. Gamboana* and *J. comitans* had been described
by Professor Martínez in 1944.

He cleared up a puzzle centering around *Cupressus thurifera* H. B. K. This species was known only from the type collection. Professor Martínez reasoned that since no specimens, other than the type, existed in any herbaria, and since no *Cupressus* was known to grow in the area from which the type of *C. thurifera* had come but "an abundance" of *J. flaccida* var. *poblana* occurred in this region, probably *C. thurifera* was *J. flaccida* var. *poblana*. This shrewd guess was completely confirmed when he examined the type of *C. thurifera!* The latter, therefore, becomes a synonym under *J. flaccida* var. *poblana*.

The paper is nicely illustrated with 108 "figures," many of which could easily have been classified as "plates" for they are made up of a number of line drawings, each separate drawing bearing a subnumber that corresponds with the numbered explanations of the figures. Over one-third of the figures are half-tone reproductions of photographs showing the general habit, character of the twigs, leaves and fruit or the nature of the bark on the mature trunks. The line drawings accurately depict the shape, arrangement and size of the leaves and fruit and the presence or absence of glands on the leaves. These drawings are refreshingly simple and accurate, without shading and clearly show the critical character.

Under each subsection Professor Martínez includes a schematic chart representing the "supposed relations" among the entities included. These charts express his ideas of the probable relationships, based wholly upon his field observations and his herbarium studies. Limits of time and funds precluded the tedious and very slow experimental type of nursery work that could give more definite criteria on the phylogenetic lines along which the Mexican junipers have developed.

The paper constitutes a substantial contribution to our knowledge of the genus *Juniperus* as it occurs in Mexico. The format and typography are good. The paper used is glazed so both the half-tones and the line drawings are reproduced clearly. This is another paper written by Professor Martínez for which we may sincerely thank him. It is one that will be valuable to any botanist interested in the flora, and particularly one interested in the gymnosperms of Mexico.—IRA L. WIGGINS, Stanford University, California.